Available online at www.sciencedirect.com
ScienceDirect
Industrial Crops and Products 25 (2007) 24–33
INDUSTRIAL CROPS AND PRODUCTS
AN INTERNATIONAL JOURNAL
www.elsevier.com/locate/indcrop

Cardinal temperatures for germination and early growth of two *Lesquerella* species

N.R. Adam[a], D.A. Dierig[a,*], T.A. Coffelt[a], M.J. Wintermeyer[a], B.E. Mackey[b], G.W. Wall[a]

[a] *USDA-ARS, U.S. Arid Land Agricultural Research Center, 21881 N. Cardon Lane, Maricopa, AZ 85239, USA*
[b] *USDA-ARS, Western Regional Research Center, 800 Buchanan Street, Albany, CA 94710, USA*

Received 24 August 2005; accepted 2 June 2006

Abstract

Lesquerella (*Lesquerella fendleri*) is a potential alternative crop that is being studied for commercial oilseed production. Understanding the minimum temperatures for germination and seedling growth is important for determining potential areas for lesquerella production. The objectives of this study were to determine the cardinal temperatures for germination and seedling growth, and to screen ecotypes for germination and growth characteristics. A temperature gradient table arrangement was used to observe seed germination over a range of temperatures, and time to germination and shoot appearance. Times to 5 mm root length and 5 mm shoot length were also measured to assess cardinal temperatures for seedling survival and growth. Two different species were examined, *L. fendleri* and a species we refer to as '*L. pallida* aff.' because it differed from typical *L. pallida* plants in chromosome number and in oil quality. We concluded that both germination and growth of *L. pallida* aff. occurred fastest at 22 °C, whereas *L. fendleri* germinated earlier at 18 °C, but grew faster at 22 °C. *L. pallida* aff. also had lower germination than *L. fendleri* over the range studied. Non-dormant seeds of improved lines of *L. fendleri* had better performance at temperatures above 22 °C than did unimproved accessions. Lines of *L. fendleri* selected for high oil content and salt tolerance had similar temperature requirements for germination except for improved line WCL-LO3, the current line being used in production. This line had optimal temperatures 6 °C higher for germination and growth than the other improved lines. Accessions of *L. fendleri* collected from elevations above 2000 m performed better at warmer temperatures, whereas those collected from elevations below 2000 m tended to perform better at cooler temperatures. Dormant seeds of *L. fendleri* germinated more quickly at low temperatures and had lower base (<3 °C) and optimal (22 °C) temperatures than non-dormant seeds (>7 °C and 28 °C, respectively). We speculate that this partial dormancy trait allows populations of *L. fendleri* to exploit a wider range of temperature conditions in the wild in order to thrive in extreme environments.

Keywords: Shoot appearance; Base temperature; Optimal temperature; *Lesquerella fendleri*; *L. pallida* aff.; New crops; Oilseed

1. Introduction

Lesquerella fendleri (Gray) Wats. is an oilseed plant of the Brassicaceae family, native to the southwest U.S. that is being improved as a potential agronomic crop (Dierig et al., 1993). *Lesquerella* species native to the western U.S. contain lesquerolic hydroxy fatty acid (C20:1-OH), which is similar to ricinoleic acid (C18:1-OH) found in castor (*Ricinus communis* L.), except for two extra carbons in chain length. The longer chain length sets lesquerella apart from castor, which is imported to the U.S. Potential applications of les-

* Corresponding author. Tel.: +1 520 316 6360; fax: +1 520 316 6330.
E-mail address: ddierig@uswcl.ars.ag.gov (D.A. Dierig).

0926-6690/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.indcrop.2006.06.001

querella oil include biodegradable lubricants, novel plastics, lithium greases, protective coatings, surfactants, drying agents, cosmetics, and pharmaceuticals (Roetheli et al., 1991). The seed meal contains antioxidants from glucosinolates to extend the oil stability (Abbott et al., 1997). Some species of *Lesquerella* have naturally occurring estolides that improve the pour points of vegetable oils, and have been used as viscosity modifiers in lubricating oils (Hayes et al., 1995). Information on environmental constraints for establishment and production is needed so regions with potential for production can be selected.

An important constraint in determining the suitability of a crop for production in a new region is the range of temperatures necessary for germination and seedling growth. As a way to approximate cardinal (minimum, maximum, and optimum) temperatures for germination and early seedling growth, measurements are typically conducted across a range of temperatures. Cardinal temperatures for germination of most crop plants tend to be similar to those of normal vegetative growth (Gardner et al., 1985). However, for some species, cardinal temperatures for germination may differ from those of root or shoot elongation (Lawlor, 1987). Windauer et al. (2004) found that base and optimal temperatures for growth of *L. fendleri* from floral bud appearance to opening of the first flower were higher than those for seedling emergence to floral bud appearance.

Lesquerella is a potential commercial crop for the southwestern U.S. It requires planting in the fall for acceptable seed yields. Seeds of *L. fendleri* weigh approximately 0.60 g per 1000 and are broadcast planted in the field and furrow irrigated (Dierig et al., 1996). The plants remain in a vegetative growth stage until March when flowering begins. Plants are combine-harvested in June.

Germination and seedling growth response to temperature can vary by species, and by seed-lots within a species. Blackshaw (1991) reported that emergence of canola (*Brassica napus* L.) was reduced at 5 °C and at 30 °C. Nykiforuk and Johnson-Flanagan (1994) found that different seed-lots of canola have different germination rates at 10 °C, but were similar to each other at 22 °C and 25 °C.

Germination and seedling growth responses to temperature also vary as a result of dormancy. Seed dormancy is a means of avoiding unfavorable environmental conditions by arresting growth and development (Evans and Cabin, 1995). Most seeds are innately dormant as soon as they develop on the mother plant and begin to lose dormancy after they have dried, which may take months (Roberts, 1988). Vegis (1964) stated that as seeds lose dormancy, the temperature range over which they are capable of germinating increases. Dormancy has been demonstrated in *L. fendleri* (Bass et al., 1966; Sharir and Gelmond, 1971; Evans and Cabin, 1995; Hyatt et al., 1999), but little has been done to assess the effects of temperature on dormant seeds of improved lines.

The objectives of this research were to determine the effect of temperature on maximum germination, the minimum temperature for germination, shoot appearance and shoot growth for several accessions and breeding lines, and two species of *Lesquerella*, as well as the optimum temperatures for each of these characters. We also wanted to understand how dormancy affects the responses of germination to temperature and to use such data to select geographical regions with potential for production.

2. Materials and methods

Two different species were used in this study, *L. fendleri* and another that originated from San Antonio Botanical Gardens (San Antonio, TX). Seed of the latter was labeled as *L. pallida*, accession A3219 although chromosome numbers, oil quality, and some morphological traits distinguished it from other plants of this species, and it still has not been taxonomically classified (unpublished data). Therefore, we refer to it as '*L. pallida* aff.' because we are unsure of its identification. Seeds originated from a wild collection and were unselected for any traits.

Eight accessions and three breeding lines of *L. fendleri* and one accession of *L. pallida* aff. were examined in a series of five experiments. The time of year seeds were collected from plants in the wild; the year seed numbers were increased; the state, country, or germplasm line of origin; and elevation of origin of the plant material are presented in Table 1. Germination and root and shoot responses to temperatures were measured to compare species, breeding lines, and accessions of *L. fendleri* originating from a range of elevations. Seeds of all *L. fendleri* accessions were collected from plants in the wild by ARS, USDA (Dierig et al., 1996; Salywon et al., 2005). The breeding lines used in this study consisted of selections for improved seed oil content, WCL-LY2 (Dierig et al., 2001b) and WCL-LO3 (Dierig et al., in press), and another for salt tolerance, WCL-SL1 (Dierig et al., 2001a).

For each experiment, 10 seeds were placed on filter paper in Petri dishes and moistened with deionized water. The Petri dishes were sealed with Parafilm to prevent the seeds from drying out and small amounts of water were added as needed. The Petri dishes were placed on the germination table in the light (fluorescent lighting, 13–14 h daily photoperiod, approximately

Table 1
Lesquerella germplasm used in germination studies

Germplasm	Genus species	Collection year	Seed increase year	Origin	Elevation of origin (m)
WCL-LO3-2003	*L. fendleri*	NA[a]	2003	High oil breeding line	NA
WCL-LO3-2004	*L. fendleri*	NA	2004	High oil breeding line	NA
A1819-2002	*L. fendleri*	1993	2002	AZ, USA	1433
A4015-2001	*L. fendleri*	1999	2001	Coahuila, Mexico	2097
A4015-2002	*L. fendleri*	1999	2002	Coahuila, Mexico	2097
A4042-2003	*L. fendleri*	2000	2003	Coahuila, Mexico	313
A4042-2004	*L. fendleri*	2000	2004	Coahuila, Mexico	313
A4048-2002	*L. fendleri*	2000	2002	Zacatecas, Mexico	1935
A4056-2002	*L. fendleri*	2001	2002	AZ, USA	1642
A4057b-2002	*L. fendleri*	2001	2002	NM, USA	2233
WCL-LY2-2002	*L. fendleri*	NA	2002	High oil breeding line	NA
WCL-LY2-2004	*L. fendleri*	NA	2004	High oil breeding line	NA
WCL-SL1-2002	*L. fendleri*	NA	2002	Salt tolerant breeding line	NA
A3219-2002	*L. pallida* aff.	1991	2002	TX, USA	NA

[a] NA, not applicable.

20 μmol m^{-2} s^{-1}). Temperature was held constant throughout each study. The temperature regime in experiments 1 and 2 ranged from 10 °C to 30 °C; experiment 3 was over the range of 9 °C to 30 °C; experiment 4 over the range of 11 °C to 32 °C; and experiment 5 was conducted over a range, 2 °C to16 °C (Table 2).

Accessions within each temperature regime for each experiment were arranged in a completely randomized design. The first three experiments had three replications within each temperature regime. To address the effect of seed storage on germination temperature, experiment 4 was conducted using lines WCL-L03-2003 (stored seed) and WCL-L03-2004 (recently harvested) with six replications. Experiment 5 was conducted at cooler temperatures, where accessions were replicated 4 times within each temperature regime. The number of seeds germi-

Table 2
Base temperature means ± standard errors (°C) for germination and growth characters of *L. pallida* aff. and *L. fendleri*[a]

Experiment	Species	Accession/breeding line	Germination	Root (5 mm)	Shoot appearance	Shoot (5 mm)
Species/line, experiment 1 (10–30 °C)	*L.pallida* aff.	A3219	8.81 ± 0.51 a		8.39 ± 0.7 a	7.42 ± 1.48
	L. fendleri	A1819	5.81 ± 0.42 b	4.32 ± 0.65	4.97 ± 0.7 b	5.16 ± 1.21
	L. fendleri	WCL-LY2 (high oil)	6.07 ± 0.42 b	5.36 ± 0.65	5.79 ± 0.7 ab	5.98 ± 1.21
	L. fendleri	WCL-SL1 (salt tolerant)	5.9 ± 0.42 b	6.09 ± 0.65	6.4 ± 0.7 ab	6.12 ± 1.21
Elevation, experiment 2 (10–30 °C)	*L. fendleri*	A1819 (1430 m)	5.81 ± 0.42	4.32 ± 0.65	4.97 ± 0.7	5.16 ± 1.21
	L. fendleri	A4056 (1641 m)	6.46 ± 0.42	5.33 ± 0.65	6.6 ± 0.7	5.77 ± 1.21
	L. fendleri	A4048 (1935 m)	4.97 ± 0.42	3.91 ± 0.65 a	4.98 ± 0.7	3.84 ± 1.21
	L. fendleri	A4015 (2097 m)	6.7 ± 0.42	5.43 ± 0.65	6.52 ± 0.7	6.79 ± 1.21
	L. fendleri	A4057b (2233 m)	6.79 ± 0.42	6.93 ± 0.65 b	7.6 ± 0.7	6.74 ± 1.21
Storage 1, experiment 3 (9–30 °C)	*L. fendleri*	WCL-LO3-2003 (stored)	3.76 ± 1.74	3.36 ± 0.67	3.18 ± 1.17	2.18 ± 1.41
	L. fendleri	WCL-LO3-2004 (fresh)	−0.52 ± 1.74	2.12 ± 0.67	4.25 ± 1.17	4.51 ± 1.15
	L. fendleri	WCL-LY2-2002 (stored)	5.02 ± 1.74 a	4.05 ± 0.67	3.43 ± 1.17	2.07 ± 1.15
	L. fendleri	WCL-LY2-2004 (fresh)	−2.23 ± 1.74 b	4.64 ± 0.67	3.92 ± 1.17	2.52 ± 1.15
	L. fendleri	A4042-2003 (stored)	6.02 ± 1.74	6.14 ± 0.67 a	5.22 ± 1.17	4.95 ± 1.15
	L. fendleri	A4042-2004 (fresh)	1.21 ± 2.14	3.21 ± 0.82 b	3.55 ± 1.44	3.46 ± 1.41
Storage 2, experiment 4 (11–32 °C)	*L. fendleri*	WCL-LO3-2003 (stored)	7.71 ± 1.07 a	5.72 ± 0.64	5.61 ± 0.55	4 ± 1.08 a
	L. fendleri	WCL-LO3-2004 (fresh)	2.73 ± 1.07 b	4.4 ± 0.64	3.97 ± 0.55	0.35 ± 1.08 b
Cool range, experiment 5 (2–16 °C)	*L. fendleri*	WCL-LO3-2003	4.71 ± 0.37 a	4.78 ± 0.83	4.17 ± 0.45 ab	3.93 ± 0.52 a
	L. fendleri	A4015-2001	7.22 ± 0.37 b	5.8 ± 0.83	5.87 ± 0.45 a	5.76 ± 0.52 b
	L. fendleri	WCL-LY2-2004	1.18 ± 0.37 c	2.96 ± 0.83	3.02 ± 0.45 b	3.35 ± 0.52 a

[a] Values within the same column and experiment followed by different letters (a–c) are significantly different at $P < 0.05$.

nated, number of roots to 5 mm (root growth), number of shoots, and number of shoots to 5 mm (shoot growth) in length were measured and counted each day for up to 21 days for the first four experiments and up to 32 days for the cool temperature experiment. Seeds were counted as germinated when the radicle protruded from the seed coat. Shoot appearance was counted when the cotyledon emerged from the seed coat.

Maximum germination (Gmax), shoot appearance (Smax), and root (R5max) and shoot (S5max) growth to 5 mm for each accession were determined at each temperature. These values were analyzed using a logit link function with SAS Proc Genmod (SAS Institute, 1999) to adjust for binomial distribution. Days to 50% germination (GD50), 50% shoot appearance (SD50) and 50% root and shoot growth to 5 mm (R5D50 and S5D50, respectively) were determined by fitting the growth curve (percent × days) for those characters. A rate was obtained for each character by taking the reciprocal (e.g., 1/GD50 for rate of germination) that was linearly regressed with temperature. The positive slope of this relationship was extrapolated to the *x*-intercept to determine basal temperature (T_b) for each character, according to the procedure of Lawlor (1987). Bonferroni's adjustment was used for mean comparisons with $\alpha = 0.05$. The rate and temperature relationships were also analyzed using a 2-phase regression (broken line) model to determine optimal temperatures (join point for the broken-line analysis) with a 95% confidence interval for each species. Confidence limits for the optimal temperatures could not be calculated for all species due to lack of data. Where data were lacking, an estimate was made based on visual assessment of the available data.

3. Results

3.1. Germination of L. pallida aff. and L. fendleri

A comparison of *L. pallida* aff. (A3219) with an unimproved accession of *L. fendleri* (A1819) and two improved lines, WCL-LY2 and WCL-SL1 showed that Gmax (Fig. 1a) and Smax (Fig. 1b) of *L. pallida* aff. were lower than those of *L. fendleri* through much of the temperature range. The improved *L. fendleri* lines and accession A1819 were similar to each other at temperatures below 25 °C. Gmax and Smax of *L. pallida* aff. and *L. fendleri* accession A1819 declined sharply at 25 °C, and *L. pallida* aff. did not germinate above that temperature. The *L. fendleri* improved lines had greater Gmax than the others at the two highest temperatures and did not differ from each other, even though they had been selected for different characteristics. Responses of R5max and S5max were similar to those of Gmax and Smax (data not shown).

L. pallida aff. took longer to reach GD50 at temperatures below 22 °C and did not reach GD50 at the high temperatures (Fig. 1c). *L. fendleri* A1819 did not reach GD50 above 22 °C. The *L. fendleri* accession and the

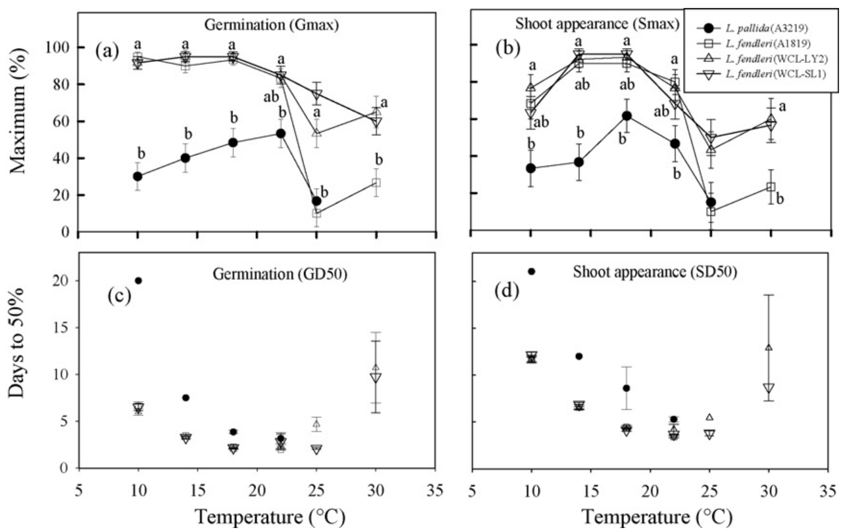

Fig. 1. Comparison of (a) maximum percent germination, (b) maximum percent shoot appearance, (c) days to 50% germination, and (d) days to 50% shoot appearance for accessions of *L. pallida* aff. (A3219) and *L. fendleri* (A1819), a line of *L. fendleri* selected and bred for high oil content (WCL-LY2), and a line of *L. fendleri* selected and bred for salt tolerance (WCL-SL1). Points within a temperature with different letters are significant at $\alpha = 0.05$. Error bars represent one standard error.

improved lines reached GD50 (Fig. 1c) and R5D50 at similar times below 25 °C (data not shown). Approximately twice as much time was required to reach SD50 (Fig. 1e), but the response patterns were similar to that of GD50. In general, GD50 was reached fastest at 18 °C by *L. fendleri* and at 22 °C by *L. pallida* aff. (Fig. 1c). However, SD50 (Fig. 1d) and R5D50 and S5D50 were attained quickest at 22 °C or above for all four lines (data not shown).

Base temperatures for germination (GTb), shoot appearance (STb), and shoot growth (S5Tb) were higher for *L. pallida* aff. than for *L. fendleri* (Table 2). Root growth of *L. pallida* aff. was poor below 18 °C, so that R5Tb could not be estimated. The accession and the improved lines of *L. fendleri* did not differ in T_b for any of the characters measured, although there was a trend of warmer T_b for the improved lines. Optimal temperatures were not estimated by broken-line analysis in this experiment. However, based on max and D50 values (maximum percentages and rates), 18 °C and 22 °C appear to be optimum for germination and growth, respectively.

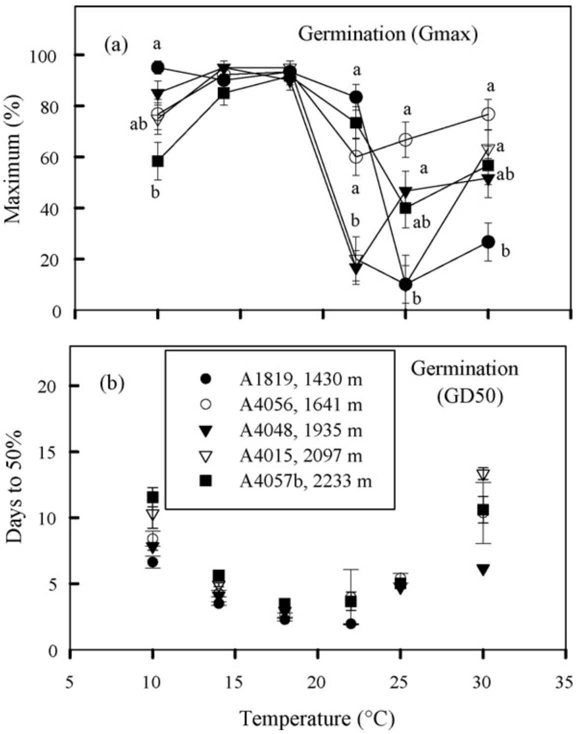

Fig. 2. Comparison of (a) maximum percent germination and (b) days to 50% germination for accessions of *L. fendleri* collected at different elevations. Points within a temperature with different letters are significant at $\alpha = 0.05$. Error bars represent one standard error.

Table 3
Optimal temperatures (°C) with lower (LL) and upper (UL) 95% confidence limits of *L. pallida* aff. and *L. fendleri* as determined by broken-line analysis

Experiment	Accession	Optimal temperature (°C)											
		Germination			Root (5 mm)			Shoot appearance			Shoot (5 mm)		
		LL	Estimated optimum	UL	LL	Estimated optimum	UL	LL	Estimated optimum	UL	LL	Estimated optimum	UL
Species/breeding line	A3219 (*L. pallida* aff.)		<22[a]			<22			<22			<22	
	A1819 (*L. fendleri*)		<22			~22			~22			~22	
	WCL-SL1 (salt tolerant)	17.7	19.8	21.6	20.4	22.3	24.1	20.2	21.3	22.3	20.6	22.3	23.9
	WCL-LY2 (high oil)	17.7	18.8	19.9	20.1	21.4	22.7	18.7	20.2	21.5	20.0	21.1	22.1
Elevation	A1819 (1430 m)		<22			<22			~22			~22	
	A4056 (1641 m)	15.7	18.6	20.7	22.5	23.8	25.0	17.9	20.6	22.8	17.1	22.1	26.0
	A4048 (1935 m)	8.0	16.2	19.7		<26			<26			<26	
	A4015 (2097 m)		>18			>18			>18			>18	
	4057b (2233 m)	18.5	20.0	21.4	21.4	22.5	23.6	19.8	20.8	21.9	20.2	21.4	22.6
Storage 2	WCL-LO3-2003 (stored)	26.0	28.0	29.7	25.2	27.8	29.7	26.1	27.5	28.6	26.4	28.0	29.3
	WCL-LO3-2004 (fresh)	20.4	22.2	23.6	21.9	22.9	23.7	18.1	22.8	25.7	21.4	22.6	23.6

[a] Estimates made by visual examination are indicated by <, > or ~.

3.2. Germination of L. fendleri accessions originating from various elevations

Accessions of *L. fendleri* collected from the lower elevations (below 2000 m) had higher Gmax (Fig. 2a) and Smax at 10 °C than those from the highest elevation (data not shown). The highest Gmax and Smax for all accessions were achieved below 20 °C. Accession A4056 (1641 m) showed the least response to temperature over the range of temperatures tested. Values of Gmax at 10 °C were similar to those at 30 °C for accessions acquired above 2000 m (Fig. 2a). Gmax was at least 40% greater at 10 °C than at 30 °C for accessions A1819 and A4048 (collected below 2000 m). Gmax and Smax of the mid-elevation accessions decreased sharply above 18 °C, whereas accessions from the highest and lowest elevations decreased more sharply at 25 °C. Gmax and Smax of all these accessions tended to be lowest between 20 °C and 28 °C.

Seeds of accessions that germinated at 30 °C progressed quickly in growth; that is, SD50 (not shown) was reached almost as quickly as GD50 (Fig. 2b). However, these seedlings were short-lived. At 10 °C, the accessions from the two highest elevations took longer than those from lower elevations to reach GD50 (Fig. 2b) and SD50 (not shown). GD50 and SD50 were lowest at 18–22 °C. The accession from the lowest elevation (A1819) did not reach 50% germination at temperatures above 22 °C. No significant differences were found among accessions for T_b (Table 2) or optimal temperature (Table 3), but there was a trend for accessions collected above 2000 m to have higher T_b.

3.3. Effect of seed storage

Seeds of *L. fendleri* accessions and improved lines that had been stored for 1 or 2 years responded differently to temperature than seeds recently harvested in 2004. The responses of WCL-LO3 are representative of the responses of all three lines or accessions (Fig. 3). Gmax was high at most temperatures for stored seed, but was reduced at higher temperatures for fresh seeds (Fig. 3a). Gmax and Smax of both improved lines tended to be greater than those of the unimproved accession A4042 (data not shown). The effect of storage on Smax at higher temperatures was reduced or absent (Fig. 3b) compared with Gmax, in the improved lines. R5max and S5max responses were similar to that of Smax (data not shown).

Recently harvested seeds reached GD50 more quickly at 10 °C than stored seeds, but took longer or did not achieve 50% germination at higher temperatures (Fig. 3c). Stored seeds performed better than recently harvested seeds at higher temperatures. This pattern was consistent for shoot appearance (Fig. 3d).

GTb and S5Tb were significantly greater for stored seeds, and there was a trend for R5Tb and S5Tb to be higher for stored seeds as well (Table 2). Optimal temperatures of germination and all growth characteristics were 5–6 °C higher for stored seeds than for fresh seeds

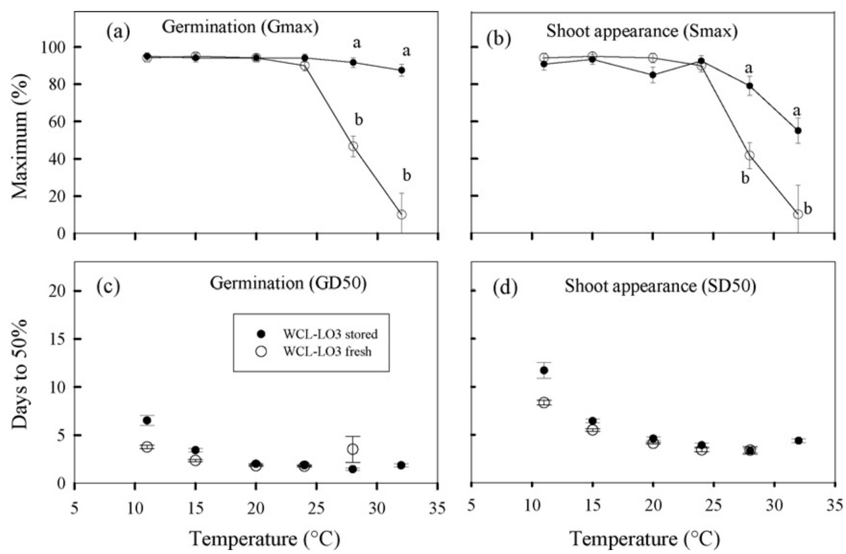

Fig. 3. Effect of storage on (a) maximum percent germination, (b) maximum percent shoot appearance, (c) days to 50% germination, and (d) days to 50% shoot appearance for an improved line (WCL-LO3) of *L. fendleri* stored for different periods of time. For maximum percent graphs, points within a temperature with different letters are significant at $\alpha = 0.05$. Error bars represent one standard error.

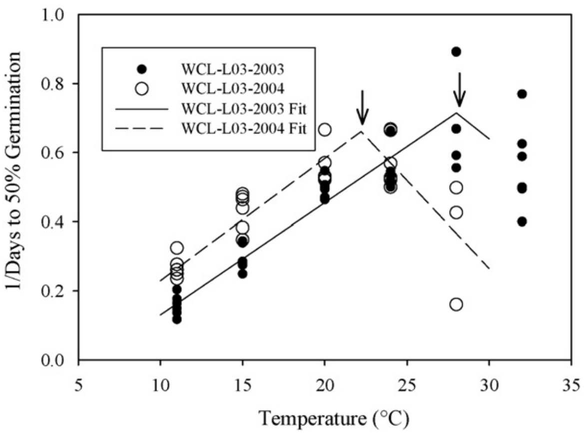

Fig. 4. Scatter plots and best-fit lines from broken-line analysis for an improved line (WCL-LO3) of *L. fendleri* comparing stored and fresh seed. Arrows indicate the join-points, or optimal temperatures.

(Table 3). The optimal temperature for germination is presented in Fig. 4.

3.4. Germination at cool temperatures

Values of Gmax and Smax (Fig. 5a and b), and for S5max (data not shown) of stored seeds of WCL-LO3 were consistently high from 8 °C and above. Values for these characters of recently harvested WCL-LY2 were consistently high above 2 °C. Maximum percentages of all characters of stored seeds of A4015 were reduced at temperatures below 11 °C. Recently harvested WCL-LY2 seeds had lower GD50 at all temperatures below 12 °C, and values for stored seeds of A4015 were greatest (Fig. 5c). Fifty percent shoot appearance was not achieved in 30 days at 2 °C and only recently harvested seeds of WCL-LY2 reached SD50 at 5 °C (Fig. 5d). The accession and breeding lines were similar for all characters at 16 °C. We also found that the germination rate versus temperature relationship for *L. fendleri* was not linear at lower temperatures (Fig. 6).

The GTb was lowest for recently harvested WCL-LY2 seeds and was the greatest for stored seeds of A4015 (Table 2). This trend was consistent for root and shoot characteristics as well.

4. Discussion

4.1. Germination of *L. pallida aff.* and *L. fendleri*

Germination and early growth at temperatures above 25 °C appear to have been improved by selection for yield related traits. *L. fendleri* germinated faster than *L. pallida* aff. at temperatures below 25 °C and also appears to be better adapted to warm temperatures. *L. pallida* aff. originates from a cooler, wetter climate, and field studies have shown that photosynthesis (Adam et al., in press) and growth (Dierig et al., 2006) are greater at a higher elevation characterized by cooler temperatures. Germination and growth of *L. fendleri* occurred more quickly at 18 °C, whereas root and shoot characters proceeded more quickly at 22 °C. This temperature shift is supported by the optimum temperatures presented in Table 3. However, all growth characteristics of *L. pallida*

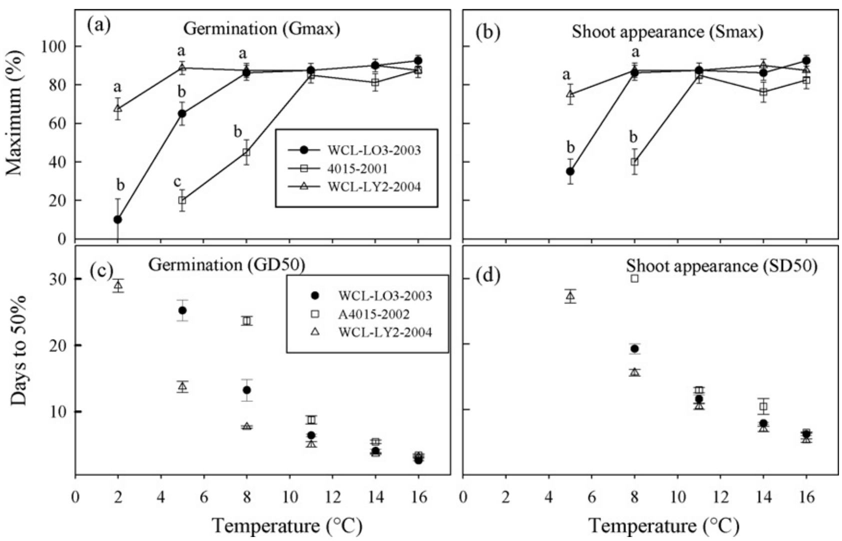

Fig. 5. Maximum percentages of (a) germination and (b) shoot appearance, and (c) days to 50% germination and (d) days to 50% shoot appearance for two breeding lines (WCL-LO3-2003 and WCL-LY2-2004) and one accession (4015-2001) of *L. fendleri*. Points within a temperature with different letters are significant at $\alpha = 0.05$. Error bars represent one standard error.

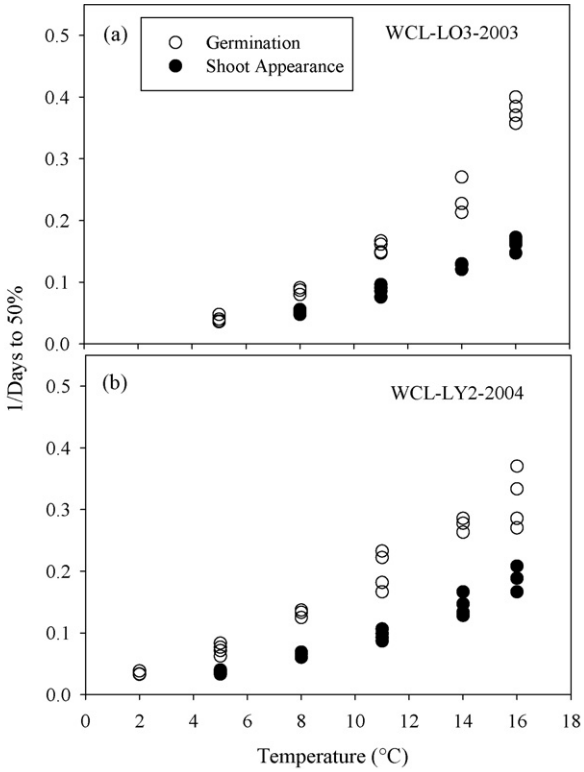

Fig. 6. Relationship of rate (1/days) and temperature for 50% germination and 50% shoot appearance for two breeding lines [(a) WCL-LO3-2003 and (b) WCL-LY2-2004] of *L. fendleri*.

aff. proceeded most rapidly at 22 °C, indicating that *L. pallida* aff. is adapted to areas with a narrower temperature range than *L. fendleri* (Nixon et al., 1983).

4.2. Germination of *L. fendleri* accessions from various elevations

Seeds of accessions originating from higher elevations were expected to be better-adapted to cooler temperatures, and those originating from lower elevations, to warmer temperatures. However, the performance of high elevation accessions was reduced at low temperatures and the lowest elevation accession did poorly at high temperatures. Possibly, the inhibition of germination at high temperatures allows the low elevation accession to postpone germination, thus protecting itself from more extreme temperatures. Similarly, the high elevation accessions may delay germination until a minimum temperature is surpassed.

Though the performance of accessions at 10 °C tended to be similar to their performance at 30 °C, there was a general decrease in maximum germination for all accessions between 18 °C and 30 °C. Brar et al. (1991) noted that germination for a variety of legume seeds was reduced at 25 °C and declined further at 30 °C. Germination in the present study was often greater at 30 °C than at 25 °C, even though it took longer to proceed. However, at 30 °C the emerged seedlings developed quickly, but also died quickly. It appears that the optimal germination temperature of these accessions, based on maximum germination and rate of germination for all of these accessions is 20 °C or less regardless of origin. This agrees with the optimum temperature estimate of 20 °C presented by Windauer et al. (2004) for early growth (emergence to floral bud appearance) of *L. fendleri*.

4.3. Effect of seed storage

In both storage experiments, seeds that had been stored a year or more under controlled laboratory conditions were compared with seeds that had been recently harvested, thus allowing dormancy in *L. fendleri* to be assessed. Hyatt et al. (1999) showed reduced first-year germination in field-stored seeds of *L. fendleri* and attributed the reduction to dormancy that our warm-temperature data supports. The speed of germination of stored and fresh (dormant) seeds at warm temperatures was similar, but maximum germination of fresh seeds was greatly reduced. However, maximum germination of both stored and fresh seeds was greater than 90% at temperatures below 25 °C (see Fig. 3). Fresh seeds germinated more quickly at low temperatures (below 25 °C) than non-dormant seeds and had lower base and optimal temperatures for germination, suggesting that the temperature requirement for germination of dormant seeds had been shifted to a cooler range than that of non-dormant seeds. Evans and Cabin (1995) discussed "predictive germination" and the potential for lesquerella seed in seed banks to respond to selective differences between different temporal or spatial environments. Dormancy in lesquerella could provide the opportunity/capacity for the seeds to germinate in cooler conditions, thus increasing the likelihood of survival of *L. fendleri* in unpredictable environments. The amount of variability for germination among fresh seeds also indicates that there is potential to improve germplasm by selecting for non-dormancy lines. During the beginning of the growing season, plants are frequently observed in the field at various stages of growth. Plants are sown in early October in Arizona and temperatures begin to cool in the following weeks. Most plants germinate between 5 days and 10 days after planting, although new plants emerge as late as January. It was previously thought that this was because seeds fell too deep below the surface causing germination to be delayed. Our results indicate that dormancy may also be delaying germination and is overcome by the cooler temperatures experienced from planting until January, causing new plants to germinate. More uniform plantings could be achieved by selecting against dormancy.

Our second seed storage experiment indicated that although the stored seeds of the breeding lines had an advantage in higher germination at warmer temperatures, other characteristics, such as shoot appearance, were not faster. However, the responses of germination and growth characteristics of the accession (A4042) were similar to each other. Seeds of the accession (A4042) from both years did not perform as well at cooler temperatures as the improved lines and the behavior of fresh seeds of the accession (A4042-2004) at 30 °C was similar to that of the accessions in the elevation experiment. Selection has had a greater effect on germination than on early shoot growth.

4.4. Germination at cool temperatures

Although base temperatures for germination of stored seeds were generally higher than those of dormant (i.e., fresh) seeds, the estimates for base temperature varied by experiment. The second storage experiment had greater precision (due to greater replication), but the estimates for base temperature of germination of WCL-LO3 in the second experiment were higher than those of the first storage experiment. Roberts (1988) indicated that plots of germination rate versus temperature are seldom linear over the entire sub-optimal temperature range, and the cool range experiment supports this (Fig. 6). Although the second storage experiment had greater precision, it was conducted at a slightly higher temperature range. Its minimum temperature of exposure was 11 °C and the extrapolated base temperature for germination of WCL-LO3-2003 was 7.7 °C. The cool range experiment showed that seeds of WCL-LO3-2003 will germinate at 5 °C and seeds of WCL-LY2-2004 (fresh/dormant seed) will germinate at 2 °C. Linear regression using only the three lowest temperatures resulted in base temperatures of germination of less than 3 °C for WCL-LO3-2003 and less than 0 °C for WCL-LY2-2004. Extrapolated base temperatures for shoot growth of WCL-LO3-2003 and WCL-LY2-2004 could be just as low. The differences between WCL-LO3-2003 and WCL-LY2-2004 in this experiment were likely another demonstration of the dormancy effect, rather than a breeding line difference.

Coffman (1923) cited the earlier undated work of Timiriazev (University of Moscow) who placed several kinds of seeds in hollows in ice cakes. After storing them surrounded by blocks of ice for 2 months, he found that some seeds of rye, wheat, cabbage, beans, and mustard had germinated and the roots were piercing the ice. Coffman (1923) also cites work showing low minimum temperatures for *Lepidium sativa* (1.8 °C), *Linuum usitatissimum* (1.8 °C), and *Sinapis alba* (0 °C). Therefore, it is likely that the minimum temperatures determined by the cooler range experiment are more accurate. The present experiment lasted for 30 days, and it is unlikely that lesquerella seeds in the field would be subjected to such low temperatures for that length of time. However, at higher elevations where snow cover can persist, seeds could be subjected to such conditions.

Despite differences in maximum percentages and base temperatures for germination and growth characteristics, differences in optimal temperatures were difficult to detect. Some accessions performed so poorly at warmer temperatures that optimal temperature could not be estimated due to lack of data. In addition, *L. fendleri* is cross-pollinated, so variability of germination and early growth is probably high. The lines in Fig. 4 were constructed from data obtained from the second seed storage experiment that had greater replication. This breeding line showed strong effects of dormancy, including reduced Gmax at warm temperatures and lower TbG in dormant (fresh) seeds. In addition, estimates of optimal temperature for dormant seeds were several degrees cooler than those of stored seeds. The germination and root and shoot growth requirements of dormant seeds were shifted to a cooler temperature range.

5. Conclusions

We conclude that *L. pallida* aff. had a narrower temperature range for optimum germination than *L. fendleri* and that germination of *L. fendleri* was higher than that of *L. pallida* aff. over the range of temperatures tested. Non-dormant (i.e., stored) seeds of improved lines tended to have better performance at warm temperatures than unimproved accessions. However, a line selected for salt tolerance (WCL-SL1) did not differ in temperature requirements from a line selected for high oil content (WCL-LY2).

Accessions of *L. fendleri* collected from elevations above 2000 m performed better at warmer temperatures, whereas those collected from elevations below 2000 m tended to perform better at cooler temperatures.

Optimum germination temperature for all accessions and almost all breeding lines of *L. fendleri* was less than 20 °C whereas optimum temperature for shoot establishment was greater than 20 °C. However, optimum temperatures for germination and shoot appearance WCL-LO3, the germplasm used in current lesquerella production, had optimal temperatures greater than 20 °C and up to 6 °C higher than other improved lines. Estimates for *L. pallida* aff. were also higher than 20 °C, but still lower than WCL-LO3 stored or fresh seed.

Dormant seeds of *L. fendleri* germinated more quickly at low temperatures and had lower base and optimal temperatures than non-dormant seeds. We believe that this allows populations of *L. fendleri* to exploit a greater range of temperature conditions.

Acknowledgments

The authors would like to thank G. Dahlquist, M. DeVore, A. Hazelton, and H. Dawson for technical support on the plant measurements and assistance and J. Replogle, M. Conley, K. Martin, R. Lee, A. Knopf, and C. Arterberry for helpful advice and assistance for the equipment and environmental control.

References

Abbott, T.P., Dierig, D.A., Foster, M.A., Nelson, J.M., Coates, W., Frykman, H.B., Carlson, K.D., Arquette, J.D., 1997. Status of lesquerella as an industrial crop. Inform 8, 1169–1175.

Adam, N.R., Dierig, D.A., Coffelt, T.A., Mackey, B.E., Wall, G.W. Elevation effects on photosynthesis of two *Lesquerella* species. Field Crops Res., in press.

Bass, L.N., Clark, D.C., Sayers, R.L., 1966. Germination experiments with seed of *Lesquerella* spp. Proc. Assoc. Official Seed Analysts 56, 148–153.

Blackshaw, R.E., 1991. Soil temperature and moisture effects on downy brome vs. winter canola, wheat, and rye emergence. Crop Sci. 31, 1034–1040.

Brar, G.S., Gomez, J.F., McMichael, B.L., Matches, A.G., Taylor, H.M., 1991. Germination of twenty forage legumes as influenced by temperature. J. Agron. 83, 173–175.

Coffman, F.A., 1923. The minimum temperature of germination of seeds. J. Am. Soc. Agron. 15, 257–270.

Dierig, D.A., Adam, N.R., Mackey, B.E., Dahlquist, G.H., Coffelt, T.A., 2006. Temperature effects on plant growth, development, and seed production of *Lesquerella fendleri* and *Lesquerella pallida* under field conditions. Ind. Crops Prod. 24, 17–25.

Dierig, D.A., Dahlquist, G.H., Tomasi, P.M. Registration of WCL-LO3 high oil *Lesquerella fendleri* germplasm. Crop Sci., in press.

Dierig, D.A., Shannon, M.C., Grieve, C.M., 2001a. Registration of WCL-SL1 salt tolerant *Lesquerella fendleri* germplasm. Crop Sci. 41, 604–605.

Dierig, D.A., Tomasi, P.M., Dahlquist, G.H., 2001b. Registration of WCL-LY2 high oil *Lesquerella fendleri* germplasm. Crop Sci. 41, 604.

Dierig, D.A., Thompson, A.E., Rebman, J.B., Kleiman, R., Phillips, B.S., 1996. Collection and evaluation of new *Lesquerella* and *Physaria* germplasm. Ind. Crops Prod. 5, 53–63.

Dierig, D.A., Thompson, A.E., Nakayama, F.S., 1993. Lesquerella commercialization efforts in the United States. Ind. Crops Prod. 1, 289–293.

Evans, A.S., Cabin, R.J., 1995. Can dormancy affect the evolution of post-germination traits? The case of *Lesquerella fendleri*. Ecology 76, 344–356.

Gardner, F.P., Pearce, R.B., Mitchell, R.L., 1985. Physiology of Crop Plants. Iowa State University Press, Ames, IA, pp. 209–245.

Hayes, D.G., Kleiman, R., Phillips, B.S., 1995. The triglyceride composition, structure, and presence of estolides in the oils of Lesquerella and related species. J. Am. Oil Chem. Soc. 72, 559–565.

Hyatt, L.A., Evans, A.S., Baskin, C.C., 1999. Annual dormancy cycles in *Lesquerella fendleri* (Brassicaceae) seeds stored under both field and laboratory conditions. Can. J. Bot. 77, 1648–1654.

Lawlor, D.J., 1987. Cardinal temperatures for growth of crops as influenced by various seed/plant characteristics. Ph.D. Dissertation, Kansas State University.

Nixon, E.S., Ward, J.R., Lipscomb, B.L., 1983. Rediscovery of *Lesquerella pallida* (Cruciferae). Sida 10, 167–175.

Nykiforuk, C.L., Johnson-Flanagan, A.M., 1994. Germination and early seedling development under low temperature in canola. Crop Sci. 34, 1047–1054.

Roberts, E.H., 1988. Temperature and seed germination. In: Long, S.P., Woodward, F.I. (Eds.), Plants and Temperature. Symp. Soc. Exp. Biol. 42, 1–23.

Roetheli, J.C., Carlson, K.C., Kleiman, R., Thompson, A.E., Dierig, D.A., Glaser, L.K., Blasé, M.G., Goodell, J., 1991. Lesquerella as a source of hydroxy fatty acids for industrial products. Growing Industrial Material Series. USDA/CSRS, Office of Agricultural Materials.

Salywon, A.M., Dierig, D.A., Rebman, J.P., Jasso de Rodríguez, D., 2005. Evaluation of new *Lesquerella* and *Physaria* (Brassicaceae) oilseed germplasm. Am. J. Bot. 92, 53–62.

SAS Institute Inc., 1999. Cary, NC, USA.

Sharir, A., Gelmond, H., 1971. Germination studies of *Lesquerella fendleri* and *L. gordonii*, with reference to their cultivation. Econ. Bot. 25, 55–59.

Vegis, A., 1964. Dormancy in higher plants. Ann. Rev. Plant Physiol. 15, 185–244.

Windauer, L.B., Slafer, G.A., Ravetta, D.A., 2004. Phenological responses to temperature of an annual and a perennial *Lesquerella* species. Ann. Bot. 94, 139–144.